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The pterodactyloids from the Purbeck Limestone Formation of Dorset

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Synopsis. The pterodactyloid fauna of the Tithonian-Berriasian Purbeck Limestone Formation of Dorset is revised taxonomically, using both previously described and new specimens. Three distinct taxa are present, namely two ctenochasmatids, *Gnathosaurus macrurus* comb. nov. based on a mandible and *Plataleorhynchus streptophorodon* gen. et sp. nov, based on a rostrum, together with an ornithocheirid '*Ornithocheirus*' sp. A, based on a second mandible. Other pterodactyloid material from Purbeck includes probable ctenochasmatid cervical vertebrae, and indeterminate pterodactyloid teeth, a radius, a metacarpal, a tibia and several wing phalanges, the latter including the type of *Doratorhynchus validus* which is a *nomen vanum*. The presence of an ornithocheirid in the Purbeck Limestone extends the history of this type of pterodactyloid back to the Jurassic-Cretaceous boundary and reinforces the view that the major diversification of this group took place in the Middle or Upper Jurassic.

INTRODUCTION

Since the middle of the nineteenth century, the Purbeck Limestone Formation has produced a rich continental vertebrate assemblage. Determinate pterosaur material has rarely been collected however, and only three isolated elements have been described or figured in the literature. Unfortunately, the taxonomic treatment of this material has not been entirely rational and it is necessary to review the systematic history of the Purbeck pterodactyloids to explain the systematic conclusions followed here. In 1868, H.G. Seeley obtained a pterodactyloid mandible and an elongate vertebra from a quarryman at a quarry near Langton Matravers, Purbeck, Dorset. Seeley (1869) listed these two specimens briefly, assigning them the name *Pterodactylus macrurus*. At this stage, Seeley believed the vertebra to be a caudal of a long-tailed pterosaur, although he assigned it to *Pterodactylus*, a short-tailed genus. Owen (1870) figured a phalanx from 'near Swanage' as the new species *Pterodactylus validus*, but made no reference to it in the accompanying text. Seeley (1875) described the mandible and vertebra under Owen's species name *validus* despite the circumstances that firstly, his own *macrurus* was the senior specific name; secondly, Owen's figure had not been accompanied by a description; and thirdly, there was no basis for associating such disparate fragments. In his description of the vertebra, Seeley vacillated between identifying it as a caudal and as a cervical. Seeley also concluded that a new generic category was required for morphological and geographical reasons, and created the genus *Doratorhynchus* for these specimens. This aggregation of the Purbeck material under the binomen

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Doratorhynchus validus has been followed by most subsequent authors e.g. Woodward & Sherborn 1890, Seeley 1901, Plieninger 1929, Wellnhofer 1978 and Howse 1986. However, Delair (1958) had reseparated Owen's and Seeley's specimens, following Lydekker (1888) in referring only the phalanx to *Ornithocheirus validus*. Curiously however, Delair retained the binomen *Doratorhynchus validus* for Seeley's two specimens, thus creating the insupportable situation of two *validus* species existing in place of one.

By 1901, Seeley had confidently reidentified the elongate vertebra as a cervical of a long-necked pterodactyloid, and noted the resemblance of this material to Solnhofen forms such as *Cycnorhamphus*, but no explicit comparisons were made. *Doratorhynchus validus* has subsequently remained in the literature as an enigmatic pterodactyloid, either placed doubtfully with the ornithocheirids, probably on the basis of the mandible (Wellnhofer 1978) or considered to be a possible early relative of the azhdarchids on the basis of the cervical vertebra (Howse 1986, Wellnhofer 1991a).

Recently, Angela C. Milner and one of the authors (ARM) recognised two undescribed pterodactyloid cranial fragments in blocks of Purbeck Limestone, in the collections of The Natural History Museum, London. The early history of the two specimens is unknown but they are recorded as having originally been part of the collection of the Corfe Castle Museum, the museum of the Purbeck Society. This collection passed to Dorset County Museum in 1894 when the Corfe Castle Museum closed (P.C. Ensom pers. comm.). It remained as a separate collection within the Dorset County Museum collections until part of it was purchased by the British Museum (Natural History) in 1958. The pterosaur specimens were subsequently shelved among the miscellaneous crocodilians, until recognised recently. Preparation and study of these two specimens has permitted a reassessment and systematic revision of the previously described Purbeck pterodactyloid material. The opportunity is also taken to record some of the other fragments of medium-large pterodactyloids collected at Purbeck over the last century. The material referred to in this work belongs to the following institutions (acronyms in parenthesis): Department of Palaeontology, The Natural History Museum (formerly British Museum (Natural History)), London (BMNH); Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich (BSPM); Dorset County Museum, Dorchester (DORCM); Sedgwick Museum, University of Cambridge (SMC).

STRATIGRAPHY

All the specimens reviewed in this work are from the Purbeck Limestone Formation of Dorset. Most were collected in quarries in the Swanage/Langton Matravers area, the exceptions being a fragmentary cervical vertebra, a metacarpal and some phalangeal material from Durlston Bay. None of the specimens is accompanied by precise data on the locality or horizon of collection. All of the Durlston Bay specimens and some from inland quarries are labelled as having been collected from the 'Middle Purbeck Beds' which, if accurate (and this is by no means certain), could mean an origin in either the Upper Lulworth Beds or the Lower Durlston Beds. The two specimens first described by Seeley lack even this horizon data and are merely recorded as deriving from the Purbeck Limestone.

Until recently, the Tithonian-Berriasian boundary (and hence the Jurassic-Cretaceous boundary) was taken as the 'Cinder Bed' (now Cinder Member), partway through the 'Middle' Purbeck Limestone Formation at the boundary of the Lulworth Beds and Durlston Beds (Casey 1963, Rawson *et al.* 1978). However, Allen & Wimbledon (1991) have pointed out that current attempts to define the base of the Berriasian with more precision may alter the horizon of this boundary within the Purbeck Limestone Formation. Whereas selection of the *Subthurmannia subalpina* Subzone as the base of the Berriasian would maintain the status quo, selection of the *Berriasella jacobi* Subzone as the base of the Berriasian would shift the Tithonian-Berriasian boundary close to the base of the Purbeck Limestone Formation. Thus at present, the pterodactyloid material discussed in this work is ambiguously Late Tithonian or Early Berriasian and is treated as such here, but should the *Berriasella jacobi* Subzone be ratified as the new base of the Berriasian, then the Purbeck Limestone Formation and its fossil assemblages would all be of Berriasian (basal Cretaceous) age.

SYSTEMATIC PALAEONTOLOGY

Order **PTEROSAURIA** Kaup, 1834
Suborder **PTERODACTYLOIDEA** Plieninger, 1901
Family **CTENOCHASMATIDAE** Nopsca, 1928

DIAGNOSIS (After Wellnhofer 1978). Pterodactyloids with elongate, anteriorly rounded snout. Food-trapping dentition composed of a large number of long, pointed, outwardly directed teeth inserted laterally in the jaw margins. The tooth-row extends back for about half the skull length.

INCLUDED GENERA. *Ctenochasma* Meyer, 1851; *Gnathosaurus* Meyer, 1834; *Huanhepterus* Dong, 1982; *Plataleorhynchus* gen. nov.

RANGE. Upper Jurassic – basal Cretaceous; Europe and China.

Genus *GNATHOSAURUS* Meyer, 1834

TYPE SPECIES. *Gnathosaurus subulatus* Meyer, 1834 from the Tithonian of Solnhofen, Bavaria, Germany.

DIAGNOSIS (After Wellnhofer 1978 with further points in parenthesis). Relatively large ctenochasmatids with long slender skulls, jaw tips spatulate and anteriorly rounded. Premaxillae bear a low sagittal crest extending from one third of the skull length behind the snout tip to the level of the orbit. Prominent dentition (30–32 teeth per ramus), extending back to the level of the anterior edge of the nasoantorbital fenestra. The anterior spatula teeth are short and anteriorly directed, the posterior spatula teeth being longer. From the 5th tooth back on each side, the teeth lengthen substantially and are anteroposteriorly directed so that each overlaps outside the tooth in front. (The posterior teeth are much shorter). Teeth are arranged to give a food-grabbing and 'fish-basket' dentition, with the teeth inserted on the lateral edge of the jaw margin and the tips inwardly directed

Naso-antorbital fenestra about twice as large as the orbit.

RANGE. Tithonian/Berriasian of Germany and England.

Gnathosaurus macrurus (Seeley) comb. nov. Figs 1, 2

1869 *Pterodactylus macrurus* Seeley: 89–90 *partim*
1875 *Doratorhynchus validus* (Owen); Seeley: 465–8 *partim* (*non* Owen 1870)
1891 *Doratorhynchus validum* (Owen); Woods: 169 *partim* (*non* Owen 1870)
1901 *Doratorhynchus validus* (Owen); Seeley: 173 *partim* (*non* Owen 1870)
1929 *Doratorhynchus validus* (Owen); Plieninger: 27–28 *partim* (*non* Owen 1870)
1958 *Doratorhynchus validus* (Owen); Delair: 70–1 *partim* (*non* Owen 1870)
1978 *Doratorhynchus validus* (Owen); Wellnhofer: 58 *partim* (*non* Owen 1870)
1986 *Doratorhynchus validus* (Owen); Howse: 318–20 *partim* (*non* Owen 1870)

LECTOTYPE. SMC J5339, the anterior region of a mandible of a medium-sized pterodactyloid, exposed in dorsal aspect (Figs 1, 2). This specimen has not previously been figured. Seeley (1869) based '*Pterodactylus*' *macrurus* on two elements, this mandible and a cervical vertebra which thus constituted the syntypes of this species. There is no reason to associate these two specimens and the vertebra could belong to either of the large ctenochasmatids described here. Although only the vertebra has been figured previously, the mandible is more critically diagnostic of a taxon, and we have accordingly selected it as the lectotype of *macrurus*.

DIAGNOSIS. Species of *Gnathosaurus* in which the spatula on the lower jaw bears 10 teeth (14 in *G. subulatus*) and in which the main series of post-spatula mandibular teeth are nearly laterally directed (antero-laterally directed in *G. subulatus*).

TYPE LOCALITY. Quarry near Langton Matravers, Purbeck, Dorset (Seeley 1875). The precise locality is not known.

HORIZON. Purbeck Limestone Formation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous. The precise horizon is not known.

DESCRIPTION. SMC J5339 comprises an incomplete mandible exposed in dorsal aspect (Figs 1, 2). The anterior region is abraded, the middle region is well preserved and the posterior ends of both rami are absent. The anterior regions of the mandibular rami coalesce with a long narrow common symphysis (Fig. 1). The length from the anterior tip of the mandible to the broken end of the longest ramus is 308 mm, the length of the symphysis is 122 mm, and the greatest width between the diverging rami is 51 mm. The anterior extremity of the symphysis is expanded into a small spatula about 22 mm wide and 23 mm long (Fig. 2A). This is rounded anteriorly but then narrows more gradually posteriorly to give an elongate shape. The spatula bears ten alveoli, five on each side. Their arrangement indicates that the spatula teeth were all directed anterolaterally. Behind the spatula, the symphysis constricts to a width of 12 mm, then widens to 25 mm at the point where the rami diverge. At this point, the rami meet at an acute angle and completely ankylose, there being no trace of a symphysial suture. The symphysial region is relatively shallow and does not appear to have been crushed *post-mortem*.



Fig. 1 *Gnathosaurus macrurus* (Seeley) comb. nov. SMC J5339, lectotype. Anterior region of mandible in dorsal aspect. Abbreviations: sp. = spatula; sym.t. = symphyseal trough. Scale = 10 mm.

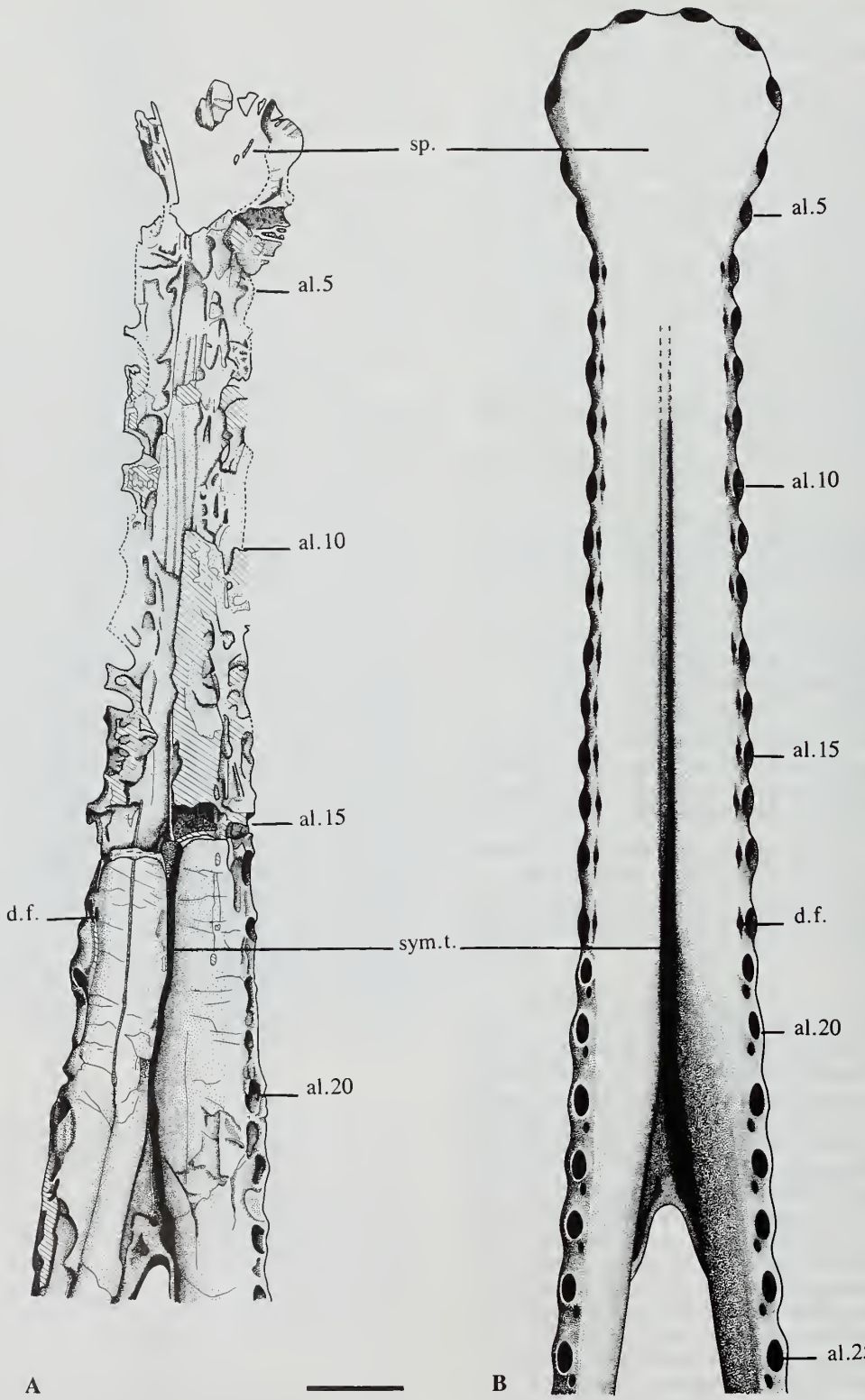


Fig. 2 *Gnathosaurus macrurus* (Seeley), comb. nov. SMC J5339, lectotype. (A) Symphyseal region as preserved. (B) Reconstruction of anterior mandible in dorsal aspect. Abbreviations: al. = alveolus; d.f. = dental foramen; sp. = spatula; sym.t. = symphyseal trough. Scale = 10 mm.

On the dorsal side of the midline of the symphysis is a symphysial trough, a groove about 2 mm wide and between 1 and 2 mm deep, with smoothly rounded edges. The trough has been slightly distorted by lateral pressure, and would have originally had the cross-section of a narrow steep-sided 'V'. The trough walls were convex in section and the floor was narrowly rounded. The trough is a narrow structure set in a relatively broad buccal floor. The trough widens over the posterior 12 mm of the symphysis, its floor becomes gently concave, and its walls merge into the ventro-medial walls of the jaw rami over the first 5 mm behind the symphysis.

A series of poorly preserved alveoli are visible on the dorsal edge of each ramus, the more complete series on the right extending back to about 50 mm behind the level of the posterior end of the symphysis. They are small and ovoid, between 1·5 and 2 mm labio-lingually and 3 mm antero-posteriorly. The alveolar rims are not raised into cylindrical collars like those of *Plataleorhynchus*, described below. Alveolus 15 on the right side is exposed in section and is deep, extending almost to the midline. Within the symphysis is a median septum of bone separating the two series of alveoli. Unlike the anterolaterally orientated spatula alveoli, those of the post-spatula region are arranged perpendicular to the midline, and the main tooth-row must have extending out sideways from the jaw. The alveoli on the spatula and anterior mandible were nearly horizontal, whereas those further back were more dorsolaterally orientated, there being a gradual gradation along the mandible. There are 29 alveoli visible on the right dentary and about 30 were probably present on each ramus (including the spatula teeth). They imply the presence of a large number of small, outwardly-directed teeth spaced evenly at approximately 3·25 mm intervals.

SYSTEMATIC POSITION. SMC J5339 is clearly the mandible of a ctenochasmatid pterodactyloid. It is shallow, has a long symphysial region and would have borne about 30 laterally or antero-laterally directed teeth of uniform cross-section on each side (Fig. 2B). The small spatula would have borne ten anterolaterally directed teeth. The buccal floor of the symphysial region has a broad flat surface curving down medially to a narrow symphysial trough. Such flattened mandibles with large numbers of evenly spaced, uniform, laterally orientated teeth are only found in the Ctenochasmatidae, although the symphysial trough appears at first to conflict with this position as it has been used as a character to define the Ornithocheiridae.

The symphysial trough has previously been reported as an ornithocheirid character (Wellnhofer 1978) but appears to have a wider distribution, although in different configurations. Ornithocheirids have either a shallow 'U'-shaped symphysial trough (*Ornithocheirus sedgwicki* and *O. daviesi*) or a wide 'V'-shaped trough (*O. machaerorhynchus* and *Brasileodactylus araripensis*). In all these forms, the buccal floor forms a narrow shelf on either side of the trough and the teeth are vertically orientated. The holotype and only mandible (BSPM AS VII 369) of the ctenochasmatid *Gnathosaurus subulatus* is preserved with ventral aspect only exposed and the presence of a trough cannot be established. However, the palate of *G. subulatus* bears a low medial ridge presumably developed from the co-ossified palatines. For the rostrum and mandibles of *G. subulatus* to occlude in a useful manner, there must have been a corresponding medial trough in the symphysial region of the mandibles of this species. The palatal ridge, though low, is sharply keeled and narrow, and the trough in SMC J5339 is of corresponding shape for such a keel to fit into. This type of keel-trough system, in which a small sharp keel and trough occur between wide palatal and buccal shelves in flattened jaws, appears to characterise some members of the Ctenochasmatidae. Thus the presence of a symphysial trough does not characterise the Ornithocheiridae *sensu latu*, but specific constructions of trough characterise separately the Ornithocheiridae and some Ctenochasmatidae.

Within the Ctenochasmatidae, SMC J5339 is closest to *Gnathosaurus subulatus* in configuration. The presence of 30 teeth per ramus is comparable to counts of 31 in *G. subulatus* and ?36–38 in *Plataleorhynchus*, but distinct from 50–90 in *Ctenochasma* and 25 in *Huanhepterus*. The small mandibular spatula bearing 10 teeth is unlikely to have been the counterpart to the large rounded rostral spatula bearing 22 teeth found in *Plataleorhynchus* and the latter bears no medial ridge that might correspond to the upper part of the ridge-trough system in *Gnathosaurus*. In shape, the spatula of SMC J5339 is comparable to that of *G. subulatus* and the latter bears a medial ridge on the palate corresponding to the symphysial trough of the mandible of SMC J5339. It is proposed that SMC J5339 be placed in the genus *Gnathosaurus* as the species *macrurus*, distinguished from *G. subulatus* by the difference in number of spatula teeth (10 in *macrurus*, 14 in *subulatus*) and the orientation of the post-spatula teeth (lateral in *macrurus*, anterolateral in *subulatus*).

Genus *PLATALEORHYNCHUS* nov.

NAME. From the Greek: *Platalea*, the generic name of the spoonbill, derived from *Platys* – flat; and *Rynchos* (latinised to *Rhynchus*) – a snout.

TYPE SPECIES. *Plataleorhynchus streptophorodon* sp. nov.

DIAGNOSIS. As for the type and only species.

RANGE. Tithonian/Berriasian of the British Isles.

Plataleorhynchus streptophorodon sp. nov. Figs 3–6

NAME. From the Greek: *streptophoros*, collar-wearing, and *odontos*, a tooth.

DIAGNOSIS. Large ctenochasmatid attaining a skull length of at least 400 mm, if *Gnathosaurus*-like proportions are assumed. Spatula roughly circular and relatively sharply demarcated from narrow rostrum posterior to it. Spatula bearing 22 teeth with shallow roots not reaching to the centre of the spatula. Anterior tip of palatines forming a slender point wedged between the two premaxillaries. Palatal face of spatula and anterior rostrum partly covered in rugose bone, indicative of the presence of a keratinous pad. No ridge on the midline of the palate. Over 62 (possibly up to 76) teeth present on entire rostrum.

HOLOTYPE. BMNH R.11957. Rostrum of a pterodactyloid visible in palatal aspect (Figs 3–5). *Ex* Corfe Castle Museum collection, purchased by BM(NH) from Dorset County Museum in 1958. Not previously described.

TYPE LOCALITY. Quarry near Langton Matravers, Purbeck, Dorset. The precise locality is not known.

HORIZON. 'Middle Purbeck Beds', Purbeck Limestone For-

mation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous. The precise horizon is not known.

DESCRIPTION. BMNH R.11957 is an incomplete section of a pterodactyloid rostrum, 174 mm long, exposed in palatal aspect, and comprising the premaxillaries, maxillaries and palatines (Figs 3, 4A). These elements are partly fused and only some sutures can be identified.

Spatula. The rostrum bears a terminal spatula which is completely flat and shows no longitudinal or transverse curvature (Fig. 5). It is formed by the premaxillaries which are completely fused in the midline. It is 39 mm long and 32 mm wide and bears 22 alveoli around its periphery. The anterior alveoli are damaged and represented by the broken edges of the bases. The remaining alveoli on the spatula are better preserved although the rims are never complete. The spatula alveoli are between 0·75 and 1·25 mm apart and all but the anterior pair are between 3·5 and 3·75 mm wide labiolingually, the anterior pair being about half this size. The alveoli in the anterior half of the spatula are anteriorly or anterolaterally orientated, those in the posterior half gradually becoming more laterally orientated. The posteriormost spatula teeth would have emerged posterolaterally from the spatula, in sharp contrast to the anterior post-spatula teeth which would have been laterally directed. In all cases, the teeth would have emerged horizontally from the edges of the jaws. The alveolar rims are formed from short raised collars of bone, which tend to coalesce with neighbouring rims on the spatula, giving it a slightly crenellated margin. Radiography of the spatula has shown that the tooth sockets within it are short and extend only partway to the middle of the spatula. Although the teeth are missing, the small size of the sockets suggests that the teeth themselves were not large or required to cope with powerful movements of prey animals.

The palatal surface of the spatula is perforated by an outer and an inner series of foramina (Fig. 5). The outer series occurs in two parallel rows of elliptical foramina close to the alveolar bases along the rostrum and forms a loop of 23 small circular openings on the spatula. This series bears a one-to-one relationship to the 22 alveoli (except for the third alveolus on the left side which has 2) and the openings are presumed to be the dental foramina. Each dental foramen is set 4–5 mm in from the nearest tooth. The inner series of foramina are larger, fewer in number (ten on the spatula) and more variable in shape. They are asymmetrically arranged with three on the left side and seven on the right side. Several emerge into shallow channels on the surface of the palate. One pair of inner foramina at the 'neck' of the spatula develop into diverging anterolaterally directed channels, while the anterior pair of foramina on the spatula each develop into forked anterolaterally directed channels separated by a V-shaped notch.

The centre of the palatal surface of the spatula is covered by a pad of rugose bone which puts out local anterolateral extensions to the periphery of the spatula (Fig. 5). Posteriorly the rugose patch becomes elongate and, at the level of the 'neck' of the spatula, it is flanked by two other elongate but irregular rugose zones. Patches of rugose bone are also present around and near the bases of the alveoli. The surface of the central rugosity consists of a dense pattern of ovoid cancellations separated by minute spans of bone. Near the periphery of the spatula these cancellations become circular pits. The non-rugose parts of the spatula are only lightly pitted, as are the outer alveolar walls and most of the palatal surface of the elongate region of the rostrum.

Post-spatula rostrum. Behind the spatula, the rostrum narrows to 15 mm in width and then gradually broadens (Figs 3, 4A). The premaxillaries extend back behind the spatula for a further 36 mm but here the medial suture is still present. Behind the premaxillaries are the fused palatines in the midline and the paired maxillaries on either side. The palatines terminate in a narrow point anteriorly and are slightly sloping to give a raised midline to the palate. The maxillary-palatine sutures are largely visible, except where damaged, but the premaxillary-maxillary sutures cannot be seen clearly. The posterior palatal shelf of each maxillary bears a long shallow trough between the alveoli and the suture with the palatine. These troughs fade out well behind the spatula. The damage to the rostrum appears to involve some anteroposterior compression or telescoping with some anteroposterior overlap of elements. The reconstruction of the rostrum (Fig. 4B) attempts to compensate for this compression, assumed to be equivalent to the space occupied by 3–4 teeth on each side.

There were at least 20 post-spatula teeth on each side and, if it is assumed that some telescoping of the rostrum has occurred and that a few more teeth were present posteriorly,

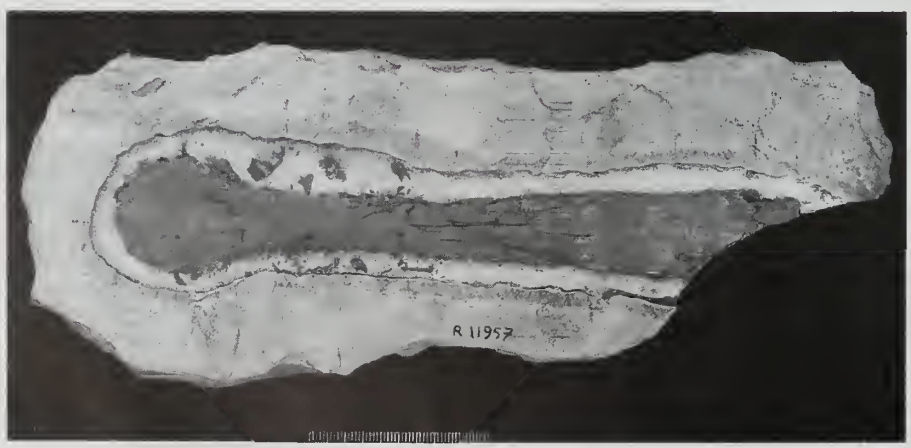
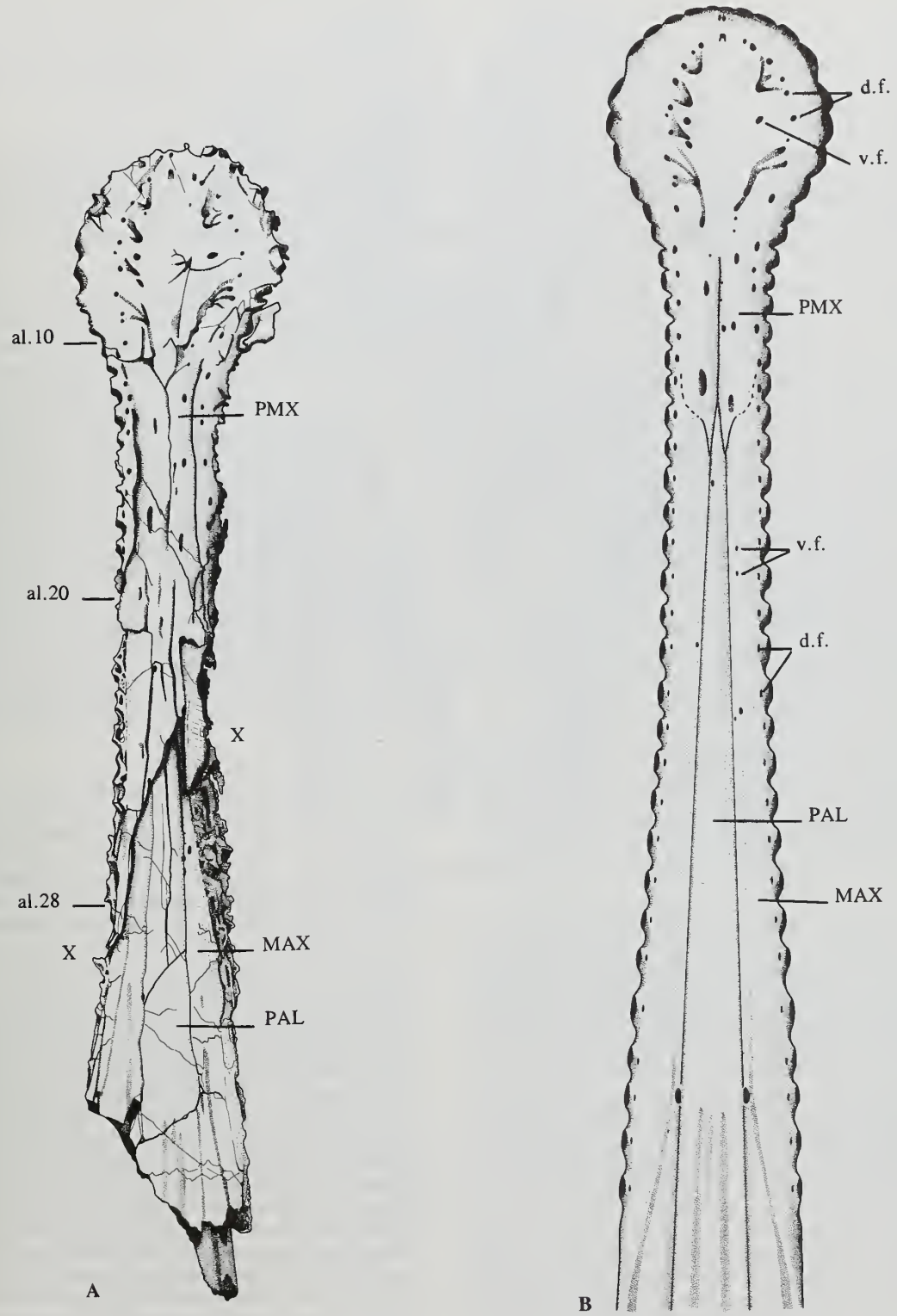


Fig. 3 *Plataleorhynchus streptophorodon* gen. et sp. nov. BMNH R.11957, holotype rostrum in palatal aspect x 0·7.



g. 4 *Plataleorhynchus streptophorodon* gen. et sp. nov. BMNH R.11957, holotype rostrum in palatal aspect. (A) Interpretive drawing. (B) Reconstruction of rostrum. The reconstruction incorporates compensation for the telescoping of the original specimen, and is therefore somewhat longer. Abbreviations: al. = alveolus; d.f. = dental foramen; MAX = Maxillary; PAL = Palatine; PMX = Premaxillary; v.f. = vascular foramen; x–x crack marking region of telescoping of specimen. Scale = 10 mm.

there might have been 5–7 more in each row (Fig. 4B reconstruction). Their alveoli are similar in size to those of the spatula teeth, but are less closely spaced with 2·5 to 3·5 mm separation, and their 'collars' show no tendency to coalesce. The dental foramina move to close proximity to the teeth behind the spatula and are incorporated into the base of the alveolar rim by tooth 17 on each side. On either side of the midline of the post-spatula rostrum are a series of large oval foramina, corresponding to the inner foramina on the spatula. Most of the palatal surface in this region is covered in delicate anteroposteriorly orientated striae, with occasional rugose patches along the midline. *The rugose palate surface.* In several groups of vertebrates, notably chelonians, birds and some ornithischian dinosaurs, the presence of a horny beak or palate is associated with a characteristic rugose surface to the bone underlying the horn-covered area. This is noticeable in the palates of many living turtles and birds, where the association between the horny beak and crushing palate and the rugose and vascular underlying bone is indisputable. Such palatal surfaces have not been previously reported in tooth-bearing pterosaurs, but are present in *Plataleorhynchus* as described here. A search through specimens available to us has revealed a slender strip of rugose bone on the anterior palate of the anhanguerid '*Ornithocheirus*' *cuvieri* from the Lower Chalk of Kent (pers. obs.) and it is likely that such structures were present in other large pterodactyloids at least. It appears that *Plataleorhynchus* had a pad of horny skin on the palatal surface of the spatula and along parts of the anterior palatal surface of the rostrum. Such horny palatal surfaces generally occur where a hard renewable surface is required by a feeding technique involving crushing or abrasion, which would cause damage to a surface that was not both hard and self-regenerating.

SYSTEMATIC POSITION. The only pterosaurs to have a rostrum with such a pronounced flat spatula and slender, laterally directed teeth are some members of the family Ctenochasmatidae, also known from the Upper Jurassic of Europe and China. *Plataleorhynchus* can be distinguished from each of the three previously described ctenochasmatids as follows:

Ctenochasma Meyer, 1851, represented by three species from Germany and France, is the type genus of the family. It is known only from relatively small specimens, lacks a spatula and has a much larger number of closely spaced teeth (100–180) in the upper jaw. Although the only rostrum of *Plataleorhynchus* is incomplete and the full rostral tooth count is unknown, it is unlikely to be much greater than 76.

Huanhepterus Dong, 1982, represented by the single species *H. quingyangensis* from China, is of suitable size, has a terminal expansion to the rostrum but is estimated to have a rostral tooth count of about 50, significantly fewer than the other ctenochasmatid genera including *Plataleorhynchus*.

Gnathosaurus Meyer, 1834, represented by *G. subulatus* from Germany and *G. macrurus* from Purbeck has a similar number of rostral teeth to *Plataleorhynchus*, but the spatula is less circular, more ovoid in ventral aspect, bears only 10–14 teeth, and the tooth orientation change between the posterior spatula dentition and the anterior post-spatula dentition is gradual. The anterior region of the spatula bears very large teeth, the roots of which extend into the middle of the spatula. There is no evidence of rugosity on the palatal surface of the spatula or rostrum. In *Plataleorhynchus*, the spatula is almost circular in plan view, bears 22 teeth and the alveoli show a very sharp demarcation in orientation at the spatula-postspatula boundary. The anterior marginal teeth of the spatula do not appear to have been large and their sockets extend only partway towards the middle of the spatula. The palatal face of the spatula and anterior rostrum are partly rugose, as described above.

Plataleorhynchus is closest to *Gnathosaurus* in general configuration but is larger and has a rostrum showing greater differentiation between the spatula and post-spatula areas. In conclusion, *Plataleorhynchus* can be argued to represent a new genus of large ctenochasmatid with a large spoonbill-like rostrum.

LIFE STYLE. Most ctenochasmatids appear to have been filter-feeders, the long rostrum bearing long laterally directed, intermeshing teeth, providing a sieve-like device for filtering small crustaceans or similar organisms from the water or mud. *Plataleorhynchus* may likewise have been a sweep-feeder like the living spoonbill *Platalea*, swinging the head from side to side and filter feeding on a large scale. It is possible that *Plataleorhynchus* may have fed in a slightly different manner, in that, compared to other large ctenochasmatids, the terminal spatula was more differentiated, the teeth were relatively smaller (to judge from the alveoli) and the palatal surface appears to have been covered by a horny surface (Fig. 6). These suggest that the animal may have used its spatula and anterior dentition to rake through mud or weed to disturb animals, then gripping and crushing slightly larger animals in the water or substratum with the horny spatula as they were disturbed. This may have been a more significant means of procuring food for this large ctenochasmatid than simply filtering water with organisms in it.

CTENOCHASMATIDAE *Incertae sedis*

CERVICAL VERTEBRAE. SMC J5340 is a middle series cervical vertebra of a pterodactyloid, exposed in dorsal aspect and dorso-ventrally crushed. The specimen was figured by Seeley (1875 fig.1 (unnumbered), 1901 fig.65) and Howse (1986 figs 8–9). It came from near Langton Matravers, Purbeck, Dorset (Seeley 1875) and probably from the same horizon as the lectotype of *Gnathosaurus macrurus*. The precise locality is not known.

SMC J5340 is either a fourth or, more probably, a fifth cervical vertebra of a long-necked pterodactyloid. It was most recently redescribed by Howse (1986) and the following is a brief summary of that description. The specimen has been crushed in a generally dorso-ventral plane with some lateral distortion, so that the apex of the neural arch has been displaced to the left of the centrum midline. The centrum is 109 mm long, but is largely obscured by the neural arch. The anterior cotyle and posterior condyle of the centrum are too crushed for much of their structure to be made out, although the posterior condyle was situated between a pair of postexapophyses, the left one of which is preserved. There is a small oval pneumatic foramen about halfway along the centrum visible on the exposed right side.

The neural arch appears to have been a low-vaulted somewhat rounded structure. It is broad-ended, tapering to a narrow waist about two-thirds of its length from the anterior. The anterior margins of the neural arch were extended into

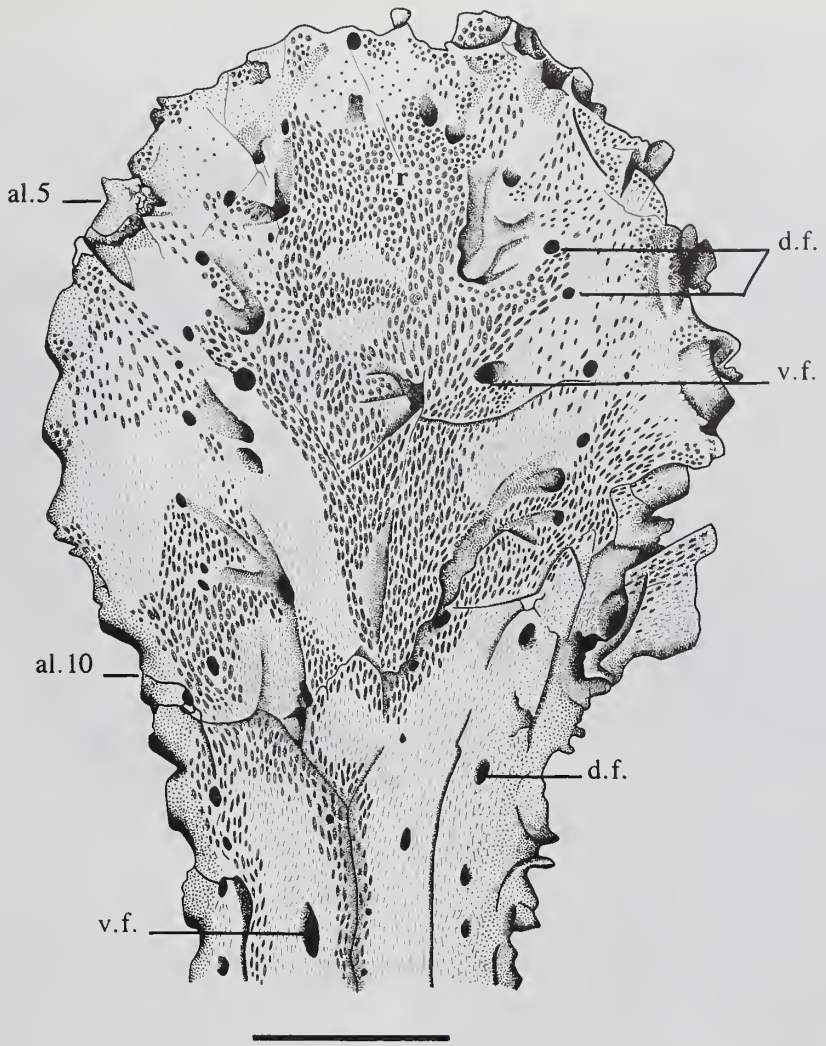


Fig. 5 *Plataleorhynchus streptophorodon* gen. et sp. nov. BMNH R.11957, spatula of rostrum in palatal aspect (interpretive drawing). Abbreviations: al. = alveolus; d.f. = dental foramen; v.f. = vascular foramen. Scale = 10 mm.

parallel, elongate, horn-like prezygapophyses, the left one of which is preserved. It bears an ovoid articular facet. The postzygapophyses, represented by a worn left structure, were broad blunt processes each bearing a distinct tubercle. The neural spine is a low slender ridge of bone running the full length of the vertebra. Fracturing at both ends suggests that it may have been slightly more raised in these regions.

BMNH 48387 (Fig. 7) is a second, incomplete, cervical vertebra which is part of the Beckles Collection, purchased in 1877. It is recorded merely as having been collected from the 'Middle Purbeck Beds' of Durlston Bay. It is a fragment comprising the posterior end of a flattened and elongate cervical vertebra similar to the above specimen. Like SMC J5340, it has a low neural spine and bears a pair of postexapophyses which bracket the posterior condyle.

These elongate cervical vertebrae clearly do not belong to an ornithocheirid, a gallodactylid or some pterodactylids. Such vertebrae are found in the Ctenochasmatidae, the Azhdarchidae and some species of *Pterodactylus*, including *P. antiquus* and *P. longicollum* (the latter two possibly synonymous according to Bennett (1993)). In recent work SMC J5340 has been treated as a fragment of a possible early azhdarchid pterodactyloid (Howse 1986, Wellnhofer 1991a). However, now that it has been established that two suitably large ctenochasmatids, *Plataleorhynchus* and *Gnathosaurus*, are present in the Purbeck Limestone Formation, the systematic position of this cervical must be reconsidered. The larger ctenochasmatid *Huanhepterus* has cervicals of similar size and proportion and this size and shape of cervical vertebra could reasonably be predicted to be present in *Plataleorhynchus*. Nevertheless, given the diversity of long-necked forms in the slightly earlier pterodactyloid fauna from the Solnhofen Limestone, such a cervical cannot be confidently assigned to a particular genus, and it is here treated as indeterminate ctenochasmatid material.

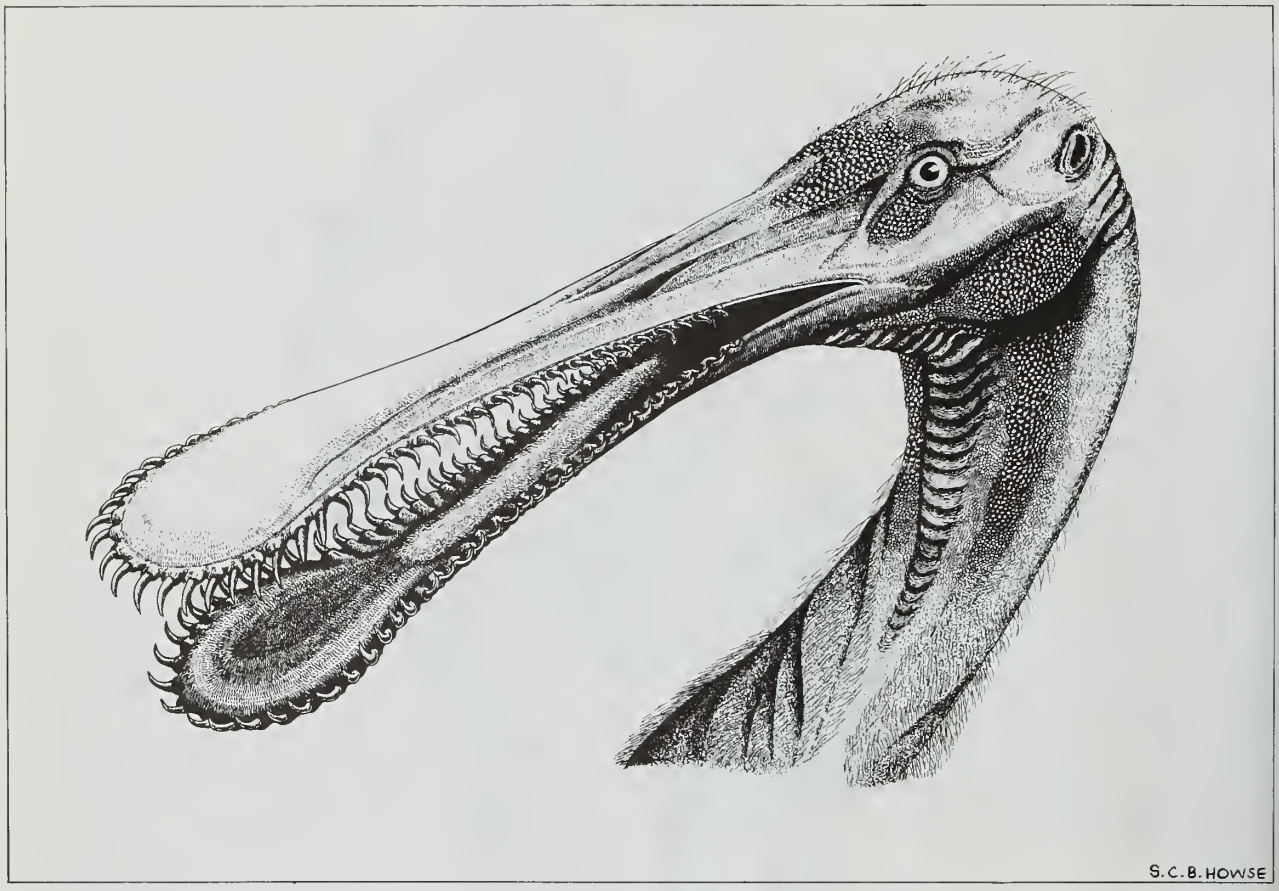


Fig. 6 Restoration of the head of *Plataleorhynchus streptophorodon*, to show relationship of spatula to the head, using the ctenochasmatids *Gnathosaurus* and *Ctenochasma* as models.

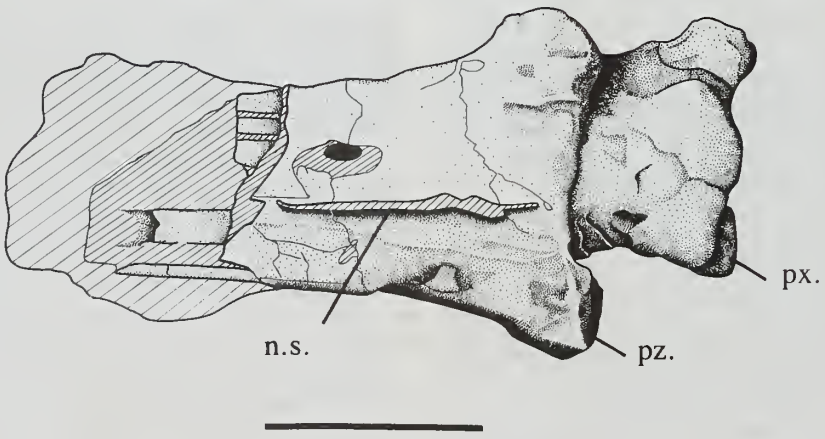


Fig. 7 Incomplete indeterminate ctenochasmatid cervical vertebra. BMNH 48387. Abbreviations: n.s. = neural spine; px. = postexapophysis; pz. = postzygapophysis. Scale = 10 mm.

Family **ORNITHOCHEIRIDAE** Seeley, 1870

SYSTEMATIC NOTE. Bennett (1989) has proposed uniting a range of advanced pterodactyloids including the ornithocheirids, pteranodontids and '*Ornithodesmus*' in one family under the name Pteranodontidae Marsh, 1876. In this work, we follow the practice of Wellnhofer (1991b) in dividing these forms into several families, pending a more comprehensive analysis of their relationships.

Genus ***ORNITHOCHEIRUS*** Seeley, 1869

TYPE SPECIES. *Ornithocheirus compressirostris* (Owen) Seeley: from the Turonian of Burham, Kent, England (see Wellnhofer 1978 pp. 55–56 for discussion of the identity of the type species of *Ornithocheirus*).

'Ornithocheirus' sp. A Fig. 8

MATERIAL. BMNH R.11958, the anterior region of a mandible of a pterodactyloid exposed in ventral aspect (Fig. 8). The specimen is somewhat crushed and the teeth have all been lost. *Ex* Corfe Castle Museum collection, purchased by BM(NH) from Dorset County Museum in 1958.

TYPE LOCALITY. 'Near Swanage', Dorset. The precise locality is not known.

HORIZON. 'Middle Purbeck Beds', Purbeck Limestone Formation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous. The precise horizon is not known.

DESCRIPTION. BMNH R.11958 comprises the anterior region of a pterodactyloid mandible exposed in ventral aspect on a block of limestone (Fig. 8). It consists of a complete elongate symphysial region and posteriorly incomplete rami, the length of the incomplete specimen being 208 mm in the midline. The symphysial region is 118 mm long and relatively narrow, passing from 9 mm width near the tip, to 20 mm width where the rami diverge. There is a slight spatulate expansion of the tip. A short section of the symphysis is visible in dorsal aspect and shows the presence of a median trough with a deep 'V'-shaped cross-section, and a few oval alveoli. The buccal shelves on either side of the trough are relatively narrow.

Most of the alveoli of the symphysial region cannot be observed directly although their lateral edges can be seen as undulations along the jaw margin, at least demonstrating that teeth were present in this region. The few alveoli visible appear to be widely spaced at intervals of about 6 mm. If this is uniform, there would be space for about 23 on each ramus. The ventral midline of the symphysial region bears a distinctive low keel. For the first 26 mm of its length, the symphysis is a flattened structure and the keel, which originates 9 mm behind the tip, is a low slender ridge about a millimetre wide and with a semicircular cross-section. For the next 35 mm, the symphysial region becomes a deeper, steeper-sided structure and the keel is a deeper ridge with a V-section merging into the sides of the mandible. For the posterior 56 mm of its length, the symphysial region is severely crushed, but the more resistant keel has resisted the crushing and forms a sharp crest extending to the back of the symphysis.

The rami are crushed outwards so that their width of 5–6 mm represents their original depth. A consequence of this crushing is that the dorsal edges face laterally and it can be



Fig. 8 '*Ornithocheirus*' species A. BMNH R.11958, anterior region of mandible in ventral aspect x 0·8.

seen that there are no alveoli behind the level of the symphysis. Crushing has splayed the rami slightly and they probably diverged less in life. The rami are broken posteriorly, anterior to the position of the articulars.

SYSTEMATIC POSITION. The discovery and description of a series of ornithocheirids, criorhynchids and anhanguerids from the Santana Formation of Brazil has resulted in the systematics of this group passing though a period of instability while new relationships and systematic criteria are defined. The Ornithocheiridae as used in recent years appears to be defined on negative criteria, and represents those members of the old Ornithocheiridae which lack the cranial outgrowths of the criorhynchids and anhanguerids. The pterodactyloid mandible described above exhibits two systematically significant characters, namely the presence of a 'V'-shaped trough extending along the midline of a symphysis, and relatively widely spaced oval alveoli. The only genera possessing these features, and an associated palatal ridge, are those until recently placed in the Ornithocheiridae *sensu latu*, but now distributed among several closely related families including the Criorhynchidae and the Anhangueridae (see Wellnhofer 1991b for a review of the taxonomy of the Brazilian members of this group). The palatal ridge and symphysial trough are known only in the Ornithocheiridae and Ctenochasmatidae and have not been described in any other Jurassic pterodactyloids, nor in *Dsungaripterus*, *Ornithodesmus*, *Noripterus*, *Pteranodon* or *Nyctosaurus*.

In the following systematic discussion, comparison is made with mandibular material of the following (sources quoted in parenthesis):

Ornithocheiridae Seeley, 1870:
'*Ornithocheirus*' [Cambridge Greensand] (personal observation)
Brasileodactylus [Santana Formation] (Kellner 1984).
Anhangueridae Campos and Kellner 1985:
Anhanguera [Santana Formation] (Wellnhofer 1991b)
Criorhynchidae Wellnhofer 1991b:
Tropeognathus [Santana Formation] (Wellnhofer 1987).

Ornithocheirus species A, represented by BMNH R.11958, has a very slight spatulate expansion, a long parallel-sided symphysis bearing a deep 'V'-shaped symphysial trough, a very low ventral V-section keel and a complete absence of ventral blades or crests. The Anhangueridae are characterized by blades and crests on the rostrum and mandible and the mandible bears a shallow 'U'-shaped symphysial trough. BMNH R.11958 is therefore not an anhanguerid. The Criorhynchidae are characterized by a massive blade of bone on the anteroventral end of the mandible and it is therefore not a criorhynchid, although the 'V'-shaped symphysial trough does occur in that family. The Ornithocheiridae is at present a residue comprising the crestless members of the old Ornithocheiridae *sensu latu*. Within the Ornithocheiridae, BMNH R.11958 most closely resembles some of the mandibular material from the Cambridge Greensand. The taxonomic status of this material has not yet been rationalized with respect to the Santana Formation pterodactyloids (that work is being undertaken by Dr D. Unwin, University of Bristol), and therefore the nomenclature of Seeley and Hooley is used in the following discussion. The Greensand specimen that most closely resembles BMNH R.11958 is the type of *Ornithocheirus machaerorhynchus* Seeley, 1870 (pl.xii, figs 1, 2), a fragment from the distal region of a mandibular symphysis

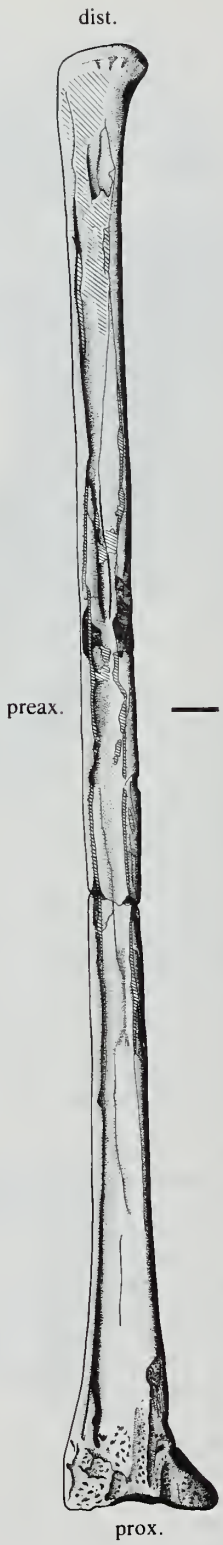


Fig. 9 *Doratorhynchus validus* (Owen) Seeley, *nomen vanum*. BMNH 40653, holotype phalanx of digit IV of right manus. Abbreviations: dist. = distal; preax. = preaxial; prox. = proximal. Scale = 10 mm.

broken at both ends. The specimen is derived from a deep symphysial region, acutely triangular in cross-section and with a ventral keel. The alveoli are oval in cross section and evenly spaced. The buccal shelves on either side of the symphysial trough are narrow, and the trough itself is deep and 'V'-shaped in cross section. No other mandibular material from the Cambridge Greensand has precisely this cross-section, but some rostral fragments bear a 'V'-shaped medial ridge on the palatal surface which appears to complement the trough in *O. machaerorhynchus*. Figured examples of such rostral fragments are the type specimens of *O. denticulatus* Seeley, 1870 (pl.xii, figs 8–9) and *O. microdon* Seeley, 1870 (pl.xii figs 6–7). Other comparable specimens described by Seeley (1870) but not figured include the type rostral fragments of *O. polyodon*, *O. nasutus*, *O. dentatus*, *O. oweni* and *O. tenuirostris*. Three specimens, the types of *O. machaerorhynchus*, *O. oweni* and *O. tenuirostris* were transferred by Hooley (1914) to the genus *Lonchodectes* while the rest were retained in *Ornithocheirus*.

Other Greensand and Chalk 'ornithocheirids' including *O. daviesi*, *O. sedgwicki*, *O. cuvieri*, *O. scaphorhynchus*, *O. platysomus* and *O. brachyrhinus*, have a shallow palatal ridge and a shallow 'U'-shaped glossal trough, quite distinct from those described above. The shallow type of trough also occurs in the Anhangueridae (but not the Criorhynchidae) and it is possible that this suite of specimens are anhanguerids.

BMNH R.11958 is significant because of its early age, but is not amenable to precise systematic placement. The absence of crests and other outgrowths, the widely spaced vertical teeth and the shape of the symphysial trough all permit it to be associated with certain of the Greensand *Ornithocheirus* 'species' of Seeley, all of which were placed by Hooley (1914) in either *Ornithocheirus* or *Lonchodectes*. It thus appears to be a member of the Ornithocheiridae *sensu stricto* and not an anhanguerid or a criorhynchid. It must be attributed to *Ornithocheirus* pending a satisfactory resolution of the systematics of that genus. Most of the named species already in the literature which incorporate or are based on comparable elements are *nomina vana* restricted to type specimens which are mandibular fragments (e.g. '*O.*' *machaerorhynchus*). In the absence of any unique diagnostic characteristics, BMNH R.11958 cannot be the basis of a new species despite its distinct stratigraphical position, and it would be misleading to refer it to *O. machaerorhynchus* on the basis of the limited similarity of mandibular fragments. Pending revision of the Greensand material, the simplest and most justifiable procedure is to record the specimen as *Ornithocheirus* 'species A'.

PTERODACTYLOIDEA *Incertae sedis*

Doratorhynchus validus (Owen) Seeley *nomen vanum* Fig. 9

1870 *Pterodactylus validus* Owen: pl.XIX, fig.7.
1875 *Doratorhynchus validus* (Owen) Seeley: 465–8 *partim*.
1888 *Ornithochirus validus* (Owen) Lydekker: 26–7.
1890 *Doratorhynchus validus* (Owen); Woodward & Sherborn: 227 *partim*.
1929 *Doratorhynchus validus* (Owen); Plieninger: 27–28 *partim*.
1958 *Ornithocheirus validus* (Owen); Delair: 71–2.
1978 *Doratorhynchus validus* (Owen); Wellnhofer: 58 *partim*.

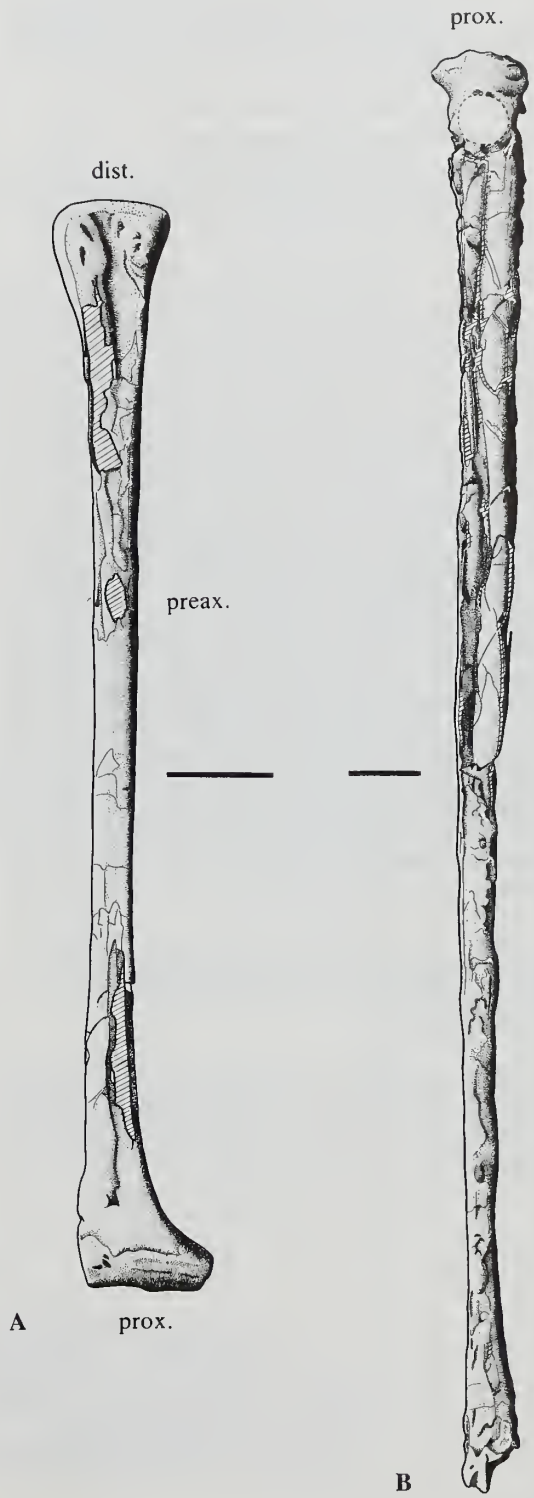


Fig. 10 Pterodactyloidea *incertae sedis*. A) BMNH 2462 right radius in ventral aspect. B) BMNH R.5798 left tibia in posterior aspect. Abbreviations as for figure 9. Scale bars = 10 mm.

The above synonymy is restricted to publications which make specific reference to the holotype phalanx.

HOLOTYPE. BMNH 40653, a first or second phalanx of digit IV (the wing-finger) of the right manus of a large pterodactyloid (Fig. 9). The specimen is exposed in dorsal aspect and was figured previously by Owen (1870 Pl.XIX, fig.7).

LOCALITY. Simply noted by Owen 1870 as 'Swanage', but probably from the Langton Matravers quarry.

HORIZON. 'Middle Purbeck Beds', Purbeck Limestone Formation; Tithonian, Upper Jurassic or Berriasian, Lower Cretaceous.

DESCRIPTION. BMNH 40653 is a crushed phalanx of digit IV (the wing-finger) of a pterodactyloid (Fig. 9). It is about 300 mm in length, with the proximal epiphysis 31 mm across and the distal epiphysis 19 mm across. There is one transverse fracture near the middle of the shaft and some superficial longitudinal fractures. The leading edge of the phalanx is straight, while the trailing edge is largely straight but curves back at each end into the posterior margins of the epiphyses. The exposed face of the bone appears to have been flat, prior to crushing, rather than of convex section, and thus probably represents the dorsal face of the phalanx. If so this was a phalanx of the right manus. The specimen was identified by Owen as the second phalanx of digit IV, and if so, would have been part of a wing finger of 1·2–1·5 metres in length. The size and extent of curvature of the distal end indicate that it was either a first or second phalanx. The shape of the proximal end resembles that of a first phalanx with the extensor process broken off. The specimen could be either a first or second phalanx of digit IV and is clearly not determinate below subordinal level. Thus the binomen *Doratorhynchus validus* is a *nomen vanum* restricted to the type specimen and no other Purbeck material can be referred to it, particularly as there are clearly at least three pterodactyloids in this assemblage.

OTHER PTERODACTYLOID MATERIAL FROM PURBECK

The following anatomically determinate pterodactyloid specimens have also been collected from the Purbeck Limestone Formation. One was recorded in Lydekker's (1888) catalogue, but several have not been mentioned in the literature.

TEETH. Ensom, Evans & Milner (1991) have reported a new microvertebrate assemblage from Sunnydown Quarry, Suttle's Quarry and other localities near Langton Matravers, Purbeck. This material includes several slender recurved pterosaur teeth (DORCM), which Ensom *et al.* identified as rhamphorhynchoid teeth, assuming them to represent the anterior fish-spearing teeth of small rhamphorhynchoids. An alternative interpretation is that they are the slender recurved marginal teeth of a large ctenochasmatid such as *Gnathosaurus* or *Plataleorhynchus*. This cannot yet be demonstrated as no intact teeth have been found with either specimen, but this would represent the most conservative interpretation of the systematic position of these teeth.

RADIUS. BMNH 2462 (Fig. 10A) is a small pterodactyloid radius from 'the Middle Purbeck of Swanage', originally in the G. A. Mantell Collection and acquired by the BM(NH) in 1838. It was listed as a phalanx by Lydekker (1888 p.27), mentioned by Wellnhofer (1978) and first identified as a radius in 1988 by S.C. Bennett (Kansas) during study of the BM(NH) collections. The radius appears to be a right element exposed in ventral aspect. It is 111 mm long, 13 mm across the proximal epiphysis, 11 mm across the distal epiphysis and 4 mm across the diaphysis at its narrowest diameter. Beyond being recognisable as a pterodactyloid radius, it is indeterminate.

METACARPAL. BMNH 48380 (Fig. 11) is a fourth metacarpal of a medium-size pterodactyloid. It formed part of the S. H. Beckles Collection and is recorded as being from the 'Middle Purbeck Beds' of Durlston Bay. It is incomplete, lacking the proximal end, but the distal end and the main shaft are about 44 mm in length, and the entire bone would have been 50–55 mm long. It bears the characteristic distal paired roller-joint articulation with the first phalanx of digit IV. The exposed semicircular articulation is smaller than the largely buried one below it, traces of which are visible. This suggests that the specimen is exposed in ventral aspect, the ventral articulation being the smaller one.

PHALANGES. DORCM G.100 is a phalanx from the 'Middle Purbeck Beds' of Langton Matravers originally belonging to the J. C. Mansell-Pleydell Collection. It was listed by Delair (1958 p.71), but is determinable only as a pterodactyloid phalanx.

BMNH 48387 is the register number for a collection of phalangeal fragments from the S. H. Beckles Collection, all originating from the 'Middle Purbeck' of Durlston Bay. Most are indeterminate, but one represents the proximal region of phalanx 1 of the wing finger – digit IV. It bears the characteristic cup-shaped proximal articulation formed partly by the extensor process.

TIBIA. BMNH R.5798 (Fig. 10B) is a large and very slender tibia collected from the Swanage area by S.L. Wood in 1919 and originally identified as a phalanx. It is 205 mm long and poorly preserved but appears to be a left tibia visible in posterior aspect. It must have belonged to a large, long-legged pterodactyloid, and may well be a ctenochasmatic tibia.

DISCUSSION

Chronological ranges of pterodactyloid families

The recognition of ctenochasmatids and ornithocheirids in the Tithonian-Berriasian of England does not significantly change our perception of the geographical distribution of these forms but does extend their known chronological ranges, and also alters the probable range of the Azhdarchidae.

The Ctenochasmatidae were already known from the Upper Jurassic of Europe. The Purbeck *Plataleorhynchus* and *Gnathosaurus* do not represent an extension to their known geographical distribution but may represent a slight chronological extension up into the earliest Cretaceous.

The Azhdarchidae, previously suggested to extend down to the base of the Cretaceous, on the basis of the cervical vertebra from Purbeck, may not appear until later in the record. The discovery of *Plataleorhynchus* does demonstrate

that ctenochasmatids as large as the Chinese *Huanhepterus* were present in Europe. *Huanhepterus* is remarkable for the extreme elongation of the middle series cervical vertebrae and it is probable, though not demonstrable, that the long cervical vertebra from Purbeck belongs to either *Gnathosaurus* or *Plataleorhynchus* and that members of both of these genera had long *Huanhepterus*-like necks. Howse (1986) suggested that the long cervical SMC J5340 from Purbeck represented an early record of an azhdarchid pterodactyloid, and that ctenochasmatids were relatives of the azhdarchids, sharing neck elongation but exhibiting it to a lesser degree. An alternative possibility is that SMC J5340 and BMNH 48387 belonged to a large ctenochasmatid and that the ctenochasmatids had entirely similar cervical series to the azhdarchids which may or may not have been present at the Jurassic-Cretaceous boundary.

The Ornithocheiridae have been described from several localities in the Cretaceous of England, the previous earliest record being *O. sagittirostris* from the Valanginian Hastings Sand of St Leonards on Sea, Sussex. The occurrence of an ornithocheirid in Tithonian-Berriasian strata is a significantly earlier record, and shows that the group was present in the uppermost Jurassic. This implies that ornithocheirids were present at the time that the Solnhofen Limestone was being deposited, and the possibility that one or more of the many Solnhofen pterodactyloids may be primitive or juvenile ornithocheirids should be explored.

Cladograms of possible pterodactyloid relationships published by Howse (1986 fig.11) and Bennett (1989 fig.3) share the conclusion that most of the higher pterodactyloids can be grouped in two major clades – the 'long-spined' forms with tall cervical neural spines (Ornithocheiridae and Pteranodontidae), and 'long-necked' forms (some Pterodactylidae, Ctenochasmatidae, Pterodaustridae and Azhdarchidae). Long-necked forms have been known from the Tithonian Solnhofen Limestone since *Pterodactylus antiquus* was first described in 1812, but the new Purbeck material confirms that the presumed 'long-spined' sister-group was also present at the Tithonian-Berriasian boundary. If Bennett's cladogram is accepted, this would also imply that those pterodactyloid families which branched off further down the cladogram – the Nyctosauridae and the Dsungaripteridae – were also present in the late Jurassic, though they are known only from Cretaceous specimens at present. The relationships of pterodactyloids are not yet so robustly established that we can draw firm conclusions about their phylogeny. However, it increasingly appears that the major family-level groups of pterodactyloids had diversified by the beginning of the Cretaceous although most are not represented until at least the Valanginian.

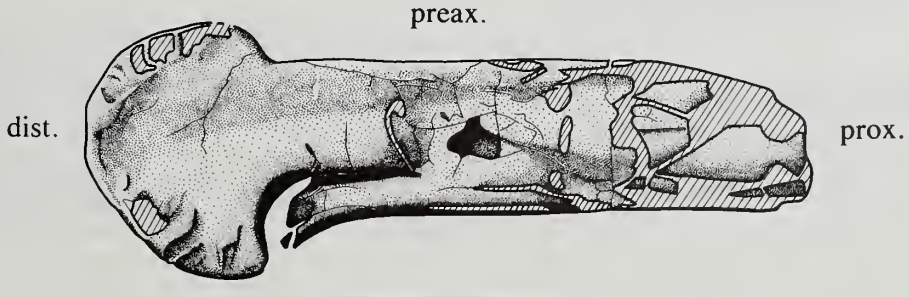
The Purbeck vertebrate fauna

The Purbeck Limestone Formation produced one of the first diverse assemblages of mid-Mesozoic continental vertebrates to be collected in the mid-19th century, principally from the Beckles Pit and Durlston Bay, and largely comprised of lizards, crocodiles, turtles, mammals and a few dinosaurs. For much of this century, little new material was collected and the known tetrapod fauna of the Purbeck Limestone Formation has remained relatively unaltered, subject to inevitable taxonomic revisions from time to time. However, recent systematic collecting of microvertebrate material from quarries around Langton Matravers by P.C. Ensom, and a series of fortuitous discoveries in the field and in museums, is adding numerous new forms to this Tithonian-Berriasian continental fauna.

The new microvertebrate assemblages collected by Ensom have proved to contain four species of lissamphibian comprising a frog, two types of salamander (one a batrachosauroidid), and an albanerpetontid (Ensom, Evans & Milner 1991), together with three new genera of multituberculate mammal (Kielan-Jaworowska & Ensom 1992; 1994). A fortuitous discovery in Durlston Bay has added the large sphenodontid *Opisthias* to the Purbeck fauna (Evans & Fraser 1994), and reassessment of older material has added the sphenodontid *Homoeosaurus* (Whiteside 1986), a new anguimorph lizard (Evans, 1994) and the pterodactyloids described in this work.

As a result of these and potential further additions, the Purbeck fauna is becoming one of the richest mid-Mesozoic continental tetrapod assemblages known, comparable to those of the Late Cretaceous of North America and Mongolia. Given that the assemblage has been collected from a restricted range of strata over a few square miles, it is likely to represent a genuine fauna of coexisting vertebrates and consequently has considerable potential for palaeoecological studies. It has always been clear that there was a substantial freshwater component to the Purbeck fauna, as evidenced by the presence of a diversity of turtles and crocodiles. The discovery of a range of lissamphibians, together with two pterodactyls specialised for feeding on small aquatic organisms, further emphasises the freshwater-marginal source of much of the fauna.

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ig. 11 Pterodactyloidea *incertae sedis*. BMNH 48380 fourth metacarpal in ventral aspect. Abbreviations as for figure 9. Scale = 10 mm.

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